



Research Article

# Mortality Patterns and Detection Bias from Carcass Data: An Example from Wolf Recovery in Wisconsin

JENNIFER L. STENGLEIN,<sup>1,2</sup> *Department of Forest and Wildlife Ecology, University of Wisconsin – Madison, 1630 Linden Drive, Madison, WI 53706, USA*

TIMOTHY R. VAN DEELEN, *Department of Forest and Wildlife Ecology, University of Wisconsin – Madison, 1630 Linden Drive, Madison, WI 53706, USA*

ADRIAN P. WYDEVEN,<sup>3</sup> *Wisconsin Department of Natural Resources, 2801 Progress Road, Madison, WI 53716, USA*

DAVID J. MLADENOFF, *Department of Forest and Wildlife Ecology, University of Wisconsin – Madison, 1630 Linden Drive, Madison, WI 53706, USA*

JANE E. WIEDENHOEFT, *Wisconsin Department of Natural Resources, 875 S 4th Avenue, Park Falls, WI 54552, USA*

NANCY K. BUSINGA,<sup>3</sup> *Wisconsin Department of Natural Resources, 2801 Progress Road, Madison, WI 53716, USA*

JULIA A. LANGENBERG,<sup>4</sup> *Wisconsin Department of Natural Resources, 2801 Progress Road, Madison, WI 53716, USA*

NANCY J. THOMAS, *United States Geological Survey – National Wildlife Health Center, 6006 Schroeder Road, Madison, WI 53711, USA*

DENNIS M. HEISEY,<sup>3</sup> *United States Geological Survey – National Wildlife Health Center, 6006 Schroeder Road, Madison, WI 53711, USA*

**ABSTRACT** We developed models and provide computer code to make carcass recovery data more useful to wildlife managers. With these tools, wildlife managers can understand the spatial, temporal (e.g., across time periods, seasons), and demographic patterns in mortality causes from carcass recovery datasets. From datasets of radio-collared and non-collared carcasses, managers can calculate the detection bias by mortality cause in a non-collared carcass dataset compared to a collared carcass dataset. As a first step, we provide a standard procedure to assign mortality causes to carcasses. We provide an example of these methods for radio-collared wolves ( $n = 208$ ) and non-collared wolves ( $n = 668$ ) found dead in Wisconsin (1979–2012). We analyzed differences in mortality cause relative to season, age and sex classes, wolf harvest zones, and recovery phase (1979–1995: initial recovery, 1996–2002: early growth, 2003–2012: late growth). Seasonally, illegal kills and natural deaths were proportionally higher in winter (Oct–Mar) than summer (Apr–Sep) for collared wolves, whereas vehicle strikes and legal kills were higher in summer than winter. Spatially, more illegally killed collared wolves occurred in eastern wolf harvest zones where wolves reestablished more slowly and in the central forest region where optimal habitat is isolated by agriculture. Natural mortalities of collared wolves (e.g., disease, intraspecific strife, or starvation) were highest in western wolf harvest zones where wolves established earlier and existed at higher densities. Calculating detection bias in the non-collared dataset revealed that more than half of the non-collared carcasses on the landscape are not found. The lowest detection probabilities for non-collared carcasses (0.113–0.176) occurred in winter for natural, illegal, and unknown mortality causes. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

**KEY WORDS** Bayesian modeling, bias correction, *Canis lupus*, carcasses, cause of mortality, detection probability, hierarchical modeling, necropsy, radio-collared, Wisconsin.

Received: 30 September 2014; Accepted: 31 May 2015

<sup>1</sup>E-mail: [jennifer.stenglein@wisconsin.gov](mailto:jennifer.stenglein@wisconsin.gov)

<sup>2</sup>Current address: Wisconsin Department of Natural Resources, 2801 Progress Road, Madison, Wisconsin 53716, USA

<sup>3</sup>Retired.

<sup>4</sup>Current address: International Crane Foundation, E11376 Shady Lake Road, Baraboo, Wisconsin 53913, USA.

Carcass recoveries are a valuable and accessible data source for understanding wildlife population dynamics. Carcass recovery data often provide known numbers of individuals that die from various causes and biological samples (e.g., teeth, jaw, reproductive tracts, hair, and tissue samples) for population modeling, diet analysis, and disease assessment (Roffe and Work 2005). Additionally, long-term records from recovered carcasses reflect changes in prominent mortality risks through time if detection and reporting biases are estimated and incorporated (Joly et al. 2009, Huso

2011, Stevens and Dennis 2013, Korner-Nievergelt et al. 2015). Translation of counts of carcasses to rigorous estimates of cause of mortality patterns and detection probability of carcasses has been pioneered by researchers studying the effect of wind turbines and other structures on bird and bat populations (Peron et al. 2013, Huso and Dalthorp 2014, Korner-Nievergelt et al. 2015). However, use of carcass recoveries for understanding variation in cause of mortality patterns and detection bias of carcasses in terrestrial wildlife populations is much less common.

In wildlife research and monitoring, datasets of carcasses that are consistently and accurately assigned to cause of mortality categories are the foundation for analysis of mortality patterns. An assumption in usual categorical data analysis is that the cause of mortality categories are mutually exclusive outcomes that are correctly identified (Agresti 2002, Congdon 2006). Carcasses with ambiguous causes of mortality must be assigned to discrete categories, but incorrect categorization will affect inference. Standardized criteria for categorization of carcasses by discrete mortality cause are necessary to ensure repeatability and reliable estimates of trend. Field observation, laboratory analysis, and necropsy of wildlife carcasses by trained professionals are the primary ways to determine causes of mortality rigorously (Roffe and Work 2005).

Estimation of cause-specific mortality rates typically involves following radio-collared or marked individuals in a population until death or recovery and determining their cause of mortality (Heisey and Fuller 1985, Schaub and Pradel 2004). These data lead to information on mortality rate and the cause-specific allocation of that rate (Heisey and Fuller 1985). However, data on the number of mortalities due to a particular cause do not need to come from a radio-collared or marked sample, and instead can come from any sample of recovered carcasses (Joly et al. 2009). A long-term dataset of recovered carcasses alone can be used to understand spatial, temporal, and demographic patterns in mortality causes. Counts of carcass data can be very useful to wildlife managers when appropriate analytic tools for understanding the patterns are made accessible. Specifically, carcass data informs the probability that given a death occurs, that death is of a particular cause (Heisey and Patterson 2006).

Carcasses recovered in different ways can have potentially different detection biases. Some carcasses are found when animals are live-captured, radio-collared, and tracked with radio-telemetry until they die. These collared carcasses provide accurate estimates of mortality rates when the collared sample is representative of the population (or cohort if the analysis includes covariates) and any collared individuals that disappear do not actually die (Pollock et al. 1989, Tsai et al. 1999). Another source of carcasses is the convenience sample of non-collared carcasses that are found on the landscape without the aid of radio-tracking. The non-collared carcasses likely do not represent population cause-specific mortality probabilities because of variable carcass detection rates from different mortality causes (Ciucci et al. 2007). For example, road kill carcasses are

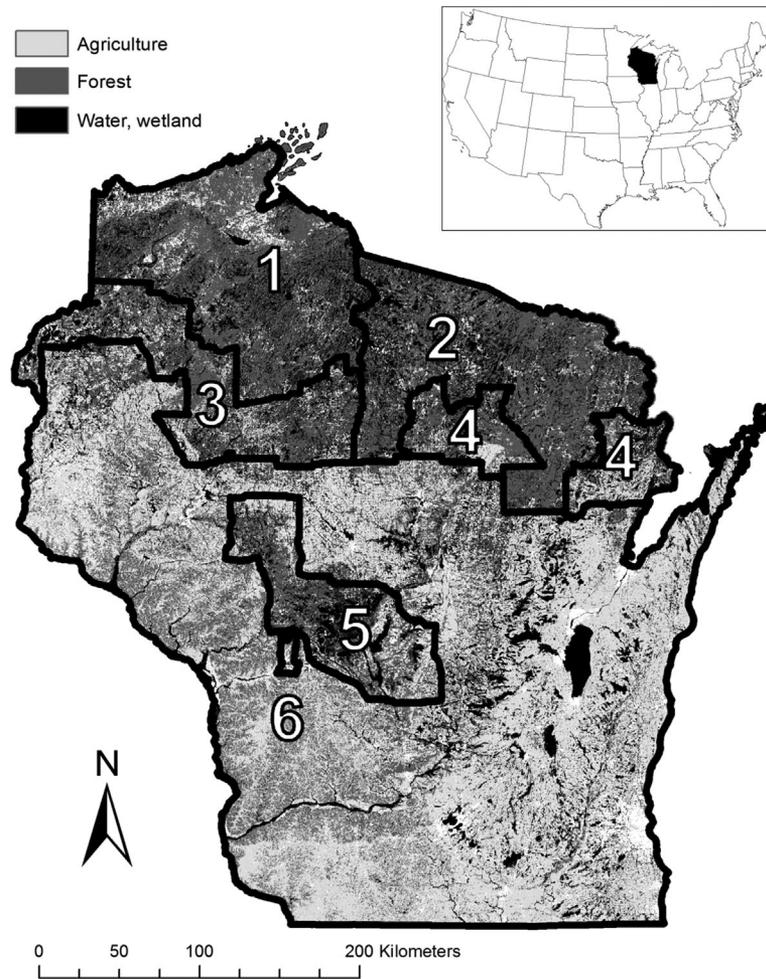
more detectable than carcasses in remote areas with disease as their mortality cause. Although collared carcasses may reflect more accurately the mortality causes in the population, non-collared carcasses also provide potentially useful information. With a sample of both collared and non-collared carcasses, it is possible to quantify biases in the non-collared carcass dataset with respect to the collared carcass dataset. Consequently, researchers and managers can use a convenience sample of non-collared carcasses to understand population parameters like cause-specific allocation of the mortality rate, detection probability of carcasses by cause, and the estimated total number of carcasses in the population.

Our goal was to develop methodology to make collared and non-collared carcass data useful to wildlife managers. Our objectives were to 1) develop a standard procedure and definitions to assign mortality cause to carcasses; 2) make accessible the methods to assess how spatial, temporal, and demographic factors influence patterns of mortality causes from recovered carcass data; and 3) develop methods to quantify the bias in the non-collared carcass sample with respect to the collared carcass sample to estimate differential detection probability for carcasses, by cause, and provide a correction from the more convenient non-collared sample to the more accurate collared sample. As a case study, we provide the first assessment of mortality patterns in the Wisconsin gray wolf (*Canis lupus*) population from >800 wolf carcasses recovered in 1979–2012. This time period covers the recolonization of wolves into Wisconsin until the first recreational harvest (Wydeven et al. 2009).

## STUDY AREA

We examined wolf carcasses in the 6 wolf harvest zones (WHZs) created for the Wisconsin wolf harvest in 2012 (Fig. 1). The WHZs corresponded roughly to habitat differences that align with variation in wolf population density. Generally, Wisconsin graded from more forest (60% forest, 6% agriculture), less urban area (0.3%), more public land (27%), and fewer roads (1.08 km road/km<sup>2</sup>) in the north (WHZ 1–4) to more agriculture (24% forest, 46% agriculture), more urban area (2.4%), less public land (3%), and more roads (1.62 km road/km<sup>2</sup>) in the south (WHZ 6, Fig. 1; Wisconsin Department of Natural Resources 1998, U.S. Geological Survey and Upper Midwest Environmental Sciences Center 2005, U.S. Department of Commerce 2010). Wolf harvest zone 5 is a forested area (46% forest, 14% agriculture) in central Wisconsin that supported 4–16 wolf packs annually (Thiel et al. 2009).

Deer were the primary prey of wolves throughout Wisconsin. Deer densities were highest in the southern portion of wolf range (central Wisconsin) because of relatively milder winters and higher interspersions of forest with agriculture. Deer hunting generally included an archery season from mid-September to early January and a 9-day firearm season during the last 2 weeks of November.



**Figure 1.** Land cover in Wisconsin, USA, from WISCLAND (Wisconsin Department of Natural Resources 1998), with the 6 wolf harvest zones created for Wisconsin wolf harvest in 2012. White areas of land cover are urban, grassland, shrubland, and barren areas.

## METHODS

### Carcass Data and Model Development

*Mortality causes from carcass data.*—To ensure repeatability, we established a procedure and a set of definitions to assign mortality cause to carcasses. Mortality cause categories, definitions, and examples were identified by wildlife necropsy specialists. We assigned a provisional mortality cause for each carcass from field investigation at the recovery site. In cases where carcasses were necropsied, we used the necropsy results to confirm, improve, or establish the mortality cause. When carcasses were not necropsied, we used the mortality cause recorded in the field. If there was doubt about the mortality cause and no necropsy, we assigned an unknown mortality cause. We determined mortality cause from necropsy rather than field investigation if there was disagreement. We used the most significant factor that led to death as the mortality cause in situations where an animal was compromised severely by one cause leading to death by another cause.

*Patterns in mortality causes.*—To understand mortality patterns in a record of carcass recovery data, we related the observed mortality causes to spatial, temporal, and demographic variables using a baseline category logit model in a

Bayesian framework (Agresti and Hitchcock 2005, Congdon 2006). The mortality cause of each carcass was a categorical response variable because it was 1 of a finite number of mortality cause categories defined for the study. Regression methods to analyze categorical data with explanatory variables focus on binomial (2 categories) and multinomial (>2 categories) logit models where the inference is on how the explanatory variables affect the probability that each category choice resulted in the observed data (mortality cause in this case; Agresti 2002, Congdon 2006). Because the probability parameters in a multinomial must sum to 1, there are 1 fewer free parameters than the number of categories that can be estimated. This constraint gets reflected in a logit model by defining 1 of the categories as the baseline and setting the parameters of the baseline category to 0 on the logit scale. For convenience, the most common category should be the baseline category; however, with appropriate translation, the results are invariant to choice of baseline category (Congdon 2006, Ntzoufras 2009). We chose to develop our model in a Bayesian framework for 2 reasons. First, Bayesian categorical data models perform better than frequentist analogs when data are sparse and there are no

observations for some covariate combinations, and this can be the case with carcass data because some mortality causes are much less prevalent in certain areas and at certain times of the year (Agresti and Hitchcock 2005). Second, the flexibility to constrain parameters under certain conditions is difficult in a frequentist model, but straightforward in a Bayesian model (Ntzoufras 2009).

The mortality cause for carcass  $r$ ,  $X_r$ , was 1 of  $K$  causes where  $K$  was the total number of causes:  $X_r = \{1, 2, \dots, K\}$ . If there are just 2 causes ( $K = 2$ ), then this model reduces to the binomial logit model (Congdon 2006). Carcasses were indexed by  $r$  where  $r = 1, 2, \dots, R$  and  $R$  was the total number of carcasses. We modeled  $X_r$  as a categorical random variable:

$$X_r \sim \text{categorical}(p_{r1}, p_{r2}, \dots, p_{rK})$$

The categorical distribution had parameters  $p_{rk}$ , which were the probabilities of carcass  $r$  having mortality cause  $k$  and  $\sum_{k=1}^K p_{rk} = 1$ . Through the logit link, the  $p_{rk}$  probabilities were related to a vector of  $z_r$  linear predictors and a vector of  $\beta_k$  unknown regression coefficients (log odds ratios; Ntzoufras 2009):

$$p_{rk} = \frac{e^{\beta_k z_r}}{\sum_{j=1}^K e^{\beta_j z_r}}$$

We set the baseline category as the most common mortality cause and the regression coefficients for  $\beta_1$  were constrained to 0 (Congdon 2006, Ntzoufras 2009). We gave all other regression coefficients normal priors with mean 0 and variance 10,000:  $\beta_k \sim \text{normal}(0, 100^2)$  where  $k = 2, 3, \dots, K$  (see R Code S1, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

*Correction between collared and non-collared carcass datasets.*—We provided a hierarchical model in a Bayesian framework to estimate cause-specific mortality rates from the collared carcass dataset, estimate detection rates of non-collared carcasses, and estimate the total number of carcasses including unobserved carcasses. To our knowledge, this is the first model that relates collared and non-collared carcass datasets for a wildlife population to estimate numerous population parameters of interest. The necessary data are a multi-year dataset with collared and non-collared carcass data with various causes of mortality, an annual estimate of the population size, and the annual number of radio-collared animals in the population (Fig. 2). The estimation of latent parameters in a wildlife population is a complex ecological problem and, therefore, it is appropriate to turn to hierarchical statistical modeling to account for multiple sources of uncertainty (Cressie et al. 2009). We chose a Bayesian approach to this problem for 4 reasons. First, Bayesian analysis allows for quantifying parameter uncertainty by estimating each parameter's value at each iteration in a Markov chain Monte Carlo (MCMC) algorithm and taking the distribution of these values as the posterior

parameter estimate (Gelman et al. 2003). Second, the multidimensional structure of observed data, unobserved processes, and prior information in hierarchical models is straightforward and convenient to build and analyze in a Bayesian framework (Royle and Dorazio 2008, Cressie et al. 2009). Third, incorporation and estimation of latent variables from the unobserved processes are more natural in Bayesian analyses compared to frequent analysis counterparts (Paap 2002, Clark 2005). Fourth, modern Bayesian software implementations make the construction of Bayesian approaches substantially more convenient than maximum likelihood approaches.

In our model, we related the observed collared and non-collared carcass counts through 4 unknown variables: 1) year-specific mortality rate for collared animals,  $c_i$ ; 2) cause-specific allocation of mortality rate for collared animals,  $m_{ik}$ ; 3) yearly number of animals that died from each cause,  $n_{ik}$ ; and 4) cause-specific detection probability of non-collared carcasses,  $d_k$ . We had models for the observed data, models for the unobserved process, and models for the parameters in the form of prior distributions (Cressie et al. 2009). Years were indexed by  $i$  where  $i = 1, 2, \dots, T$  and  $T$  was the total number of years.

Our data models were for each of our 3 observed variables. First, we defined the number of collared carcasses that were found dead in year  $i$  from cause  $k$ ,  $R_{ik}$  (categorical data), to be multinomially distributed with  $m_{ik}$  proportion of all carcasses in  $i$  that were assigned to  $k$  cause and  $R_i$  total collared carcasses (Agresti and Hitchcock 2005):

$$R_{ik} \sim \text{multinomial}(R_i, m_{i1}, m_{i2}, \dots, m_{iK}).$$

Second, we defined the total collared carcass count in year  $i$ ,  $R_i$ , as a binomial distribution with  $c_i$  year-specific collared mortality rate and  $E_i$  collared animals:  $R_i \sim \text{binomial}(E_i, c_i)$ .

We let  $E_i$  be the number of collared animals that were actively monitored at the start of period  $i$ . Third, we defined the number of non-collared carcasses that were found dead in year  $i$  from cause  $k$ ,  $V_{ik}$ , to be binomially distributed with  $D_{ik}$  probability that the carcasses were detected in the non-collared sample and  $n_{ik}$  total carcasses:

$$V_{ik} \sim \text{binomial}(n_{ik}, d_{ik}).$$

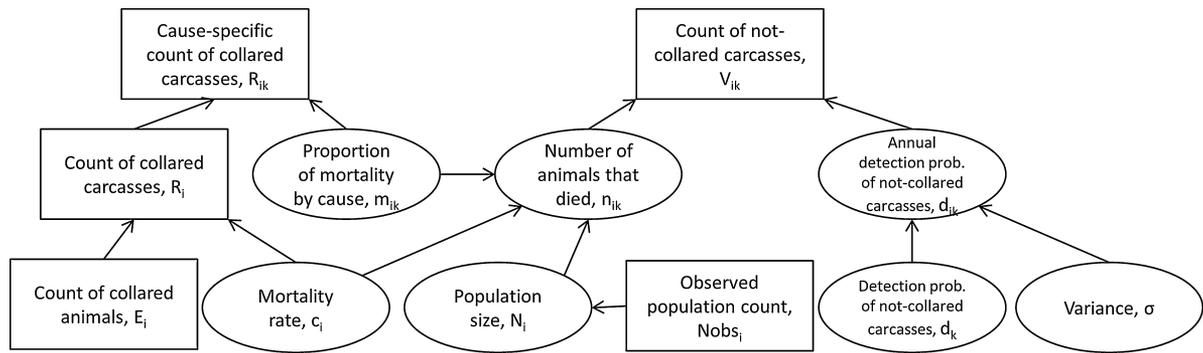
We modeled year-specific  $d_{ik}$  as distributed normally around mean  $d_k$  and unknown variance  $\sigma^2$ :

$$d_{ik} \sim \text{Normal}(d_k, \sigma^2).$$

We modeled the number of animals that died in year  $i$  from cause  $k$ ,  $n_{ik}$ , as a latent variable with a binomial distribution with probability parameter,  $c_i \times m_{ik}$ , and population size  $N_i$ :

$$n_{ik} \sim \text{binomial}(N_i, c_i \times m_{ik}).$$

We restricted  $n_{ik}$  to be an integer at least as big as the observed number of carcasses,  $R_{ik} + V_{ik}$ . The probability parameter,  $c_i \times m_{ik}$ , was the cause-specific collared mortality probability with  $c_i$  as the total collared mortality probability (non-cause-specific) and  $m_{ik}$  as the proportion of total



**Figure 2.** Directed acyclic graph (DAG) of Bayesian hierarchical model of correction between collared and non-collared carcass datasets.

collared mortality due to cause  $k$  (Joly et al. 2009). The population size,  $N_i$ , was drawn from a Poisson distribution with its mean and variance parameter equal to the population count in year  $i$ ,  $N_{obs_i}$ :

$$N_i \sim \text{Poisson}(N_{obs_i}).$$

We assigned the  $m_{ik}$ s vague Dirichlet priors:  $m_{ik} \sim \text{Dirichlet}(\alpha_{ik})$ ,  $\alpha_{ik} = 1/K$ , and we assigned  $c_{ik}$  and  $d_{jk}$  vague beta priors:  $c_{ik} \sim \text{beta}(1, 1)$  and  $d_{jk} \sim \text{beta}(1, 1)$  (Geisser 1984, Agresti 2002). The Dirichlet and beta priors are conjugate priors to the multinomial and binomial likelihoods, respectively, and therefore convenient and conventional choices for prior distributions (Gelman et al. 2003, Agresti and Hitchcock 2005). The prior on  $\sigma$  to estimate a year effect of detection probability was a uniform distribution:  $\sigma \sim \text{uniform}(0, 100)$  (see R Code S2, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com); Gelman et al. 2003).

### Case Study

**Dataset.**—We defined 3 periods of wolf recovery to align with population growth rates and management changes in Wisconsin: 1) the recovery period included 1979–1995 when the wolf population was federally listed as endangered and there was little population growth (Van Deelen 2009, Wydeven et al. 2009); 2) the early growth period included 1996–2002 when the wolf population approached the management goal of 350 wolves (Wydeven et al. 2009); and 3) the late growth period included 2003–2012 when Wisconsin used lethal methods to alleviate livestock depredation risk and human safety concerns during 3 separate delisting periods (Ruid et al. 2009).

We used collared and non-collared wolf carcasses found by Wisconsin Department of Natural Resources (WDNR) in October 1979–March 2012 (Wydeven et al. 2009). Collared wolf carcasses were located from ground-based telemetry of radio-collared wolves whose collars emitted mortality signals after 5.5 to 6 hours of inactivity. Pups were not collared unless they were  $>4$  months old and weighed  $>14$  kg (Wydeven et al. 2009). Therefore, our sample of collared pups represents wolves from 4 months to 1-year old and does not represent patterns in carcass data for very young pups. We removed 3 collared female carcasses because we suspected ( $n = 1$ ) or determined through genetic analysis

( $n = 2$ ) that they were wolf-domestic dog hybrids. Wolf trapping and handling occurred under oversight by the WDNR Animal Care and Use Committee. Our second dataset was the convenience sample of 708 non-collared wolf carcasses that were found by WDNR directly or after receiving a report of a non-collared wolf carcass. We removed 32 carcasses because we suspected ( $n = 22$ ) or determined through genetic analysis ( $n = 10$ ) that they were hybrids, and we removed 6 carcasses because of missing date or location information. Of the remaining 668 non-collared carcasses, there were 337 males, 278 females, and 53 for which sex was not determined (because of severe trauma, advanced decomposition, scavenging).

**Mortality causes from carcass data.**—A necropsy was conducted for 539 carcasses by veterinary pathologists at the United States Geological Survey (USGS) National Wildlife Health Center (primarily carcasses retrieved in 1979–2007) or WDNR (primarily carcasses retrieved in 2004–2012). Necropsy evaluations generally included whole body radiography (specifically to detect evidence of gunshot), inspection for gross pathology, and sometimes histopathology and specific laboratory analyses for evidence of viral, bacterial, parasitic, or toxin-associated disease. Our natural-cause categories were as follows: 1) infectious disease, 2) intraspecific strife, or 3) other natural causes (Table 1). Human-associated mortality causes were as follows: 4) illegal kill, 5) legal kill, 6) vehicle strike, or 7) other human causes. We categorized the remaining carcasses as unknown: 8) undetermined or unclear, and 9) trauma from an unknown source (Table 1). In our analysis, we used a reduced set of categories: natural (i.e., disease, intraspecific strife, and other natural causes), illegal kill, legal kill, vehicle strike, and unknown and other (including unknown, other human-caused mortality, other trauma; Table 1).

**Patterns in mortality cause.**—Our predictor variables,  $z_r$ , were age and sex categories (adult male, adult female, yearling, pups), seasons, periods (recovery: 1979–1995, early growth: 1996–2002, late growth: 2003–2012), and WHZ. Sample sizes for yearlings and pups were too small to consider sex differences in these categories. We defined summer and winter seasons. Summer included all carcasses found from 1 April to 30 September and covered denning, birth and rearing of pups, and early movement of the nearly grown pups with the pack (Mech and Boitani 2003). Winter

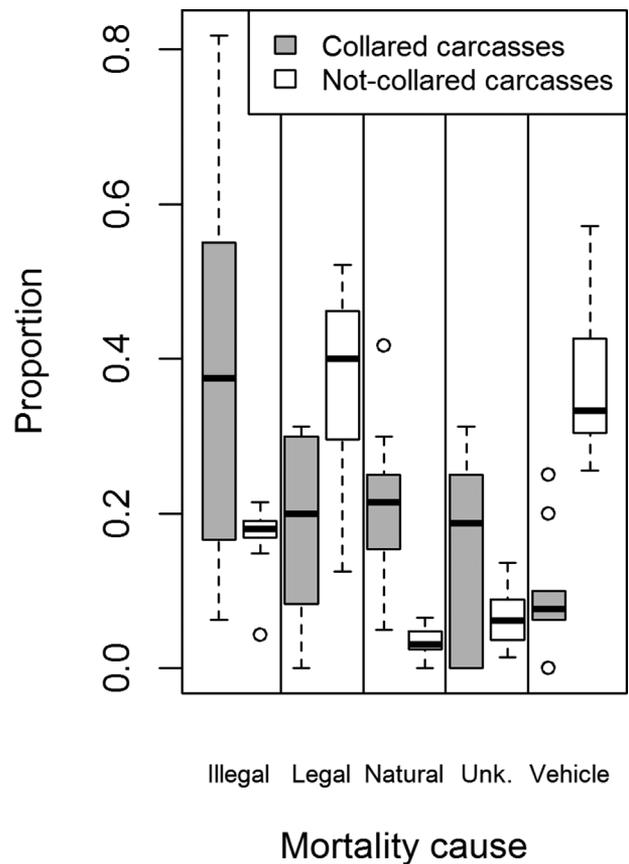
**Table 1.** Definitions and examples of 9 mortality causes for wolves found dead in Wisconsin, USA from 1979 to 2012.

Mortality cause	Category	Definition	Examples
Disease	Natural	Wolves that died from an infectious disease.	Sarcoptic mange, canine distemper, bacterial infection, blastomycosis, pneumonia, canine parvovirus
Illegal	Human	Wolves that were killed illegally by humans.	Shooting, trapping (not for research), poisoning, clubbing
Intraspecific strife	Natural	Wolves that were killed by other wolves.	Depredation control (attack of livestock, threat to humans or pets), died during capture for research or monitoring
Legal	Human	Wolves that were killed legally by humans.	
Other human causes	Human	Wolves that were killed by other human causes or a human cause that could not be identified.	Snowmobile or train collision, unintentionally entrapped by unnatural structures (pail, bear bait log), artillery fire on military base
Other natural causes	Natural	Wolves killed by other natural causes or a natural cause that could not be identified.	Starvation, drowning, stuck in crotch of tree
Other trauma	Unknown	Wolves that died from trauma. The trauma could not be ascribed to a particular source, or even to a human or natural cause category.	Severe decomposition or scavenging of a carcass that prevented mortality cause determination, more than 1 suspected mortality cause
Unknown causes	Unknown	Wolves that were found dead without a clear cause of death.	
Vehicle	Human	Wolves that were killed by a car, truck, or motorcycle on the road	

included all carcasses found from 1 October to 31 March and covered the main dispersal period, nomadic movement of packs, and mating season (Mech and Boitani 2003). We had a total of 15 variables in 4 categories. We constrained the model so that the intercept corresponded to adult male wolves in late growth period in summer in WHZ 1. Therefore, the length of vector  $z_r$  was 11 (15 predictor variables minus 4 categories) plus 1 for the intercept.

We ran 1 model where the collared carcasses were the response variable, and 1 model where the non-collared carcasses were the response variable. We did not run a model with collared carcasses and non-collared carcasses together because we expected that there were substantial differences in cause-specific detection probabilities in these datasets (Fig. 3). We removed observations in WHZ 6 from the collared carcass analysis ( $n = 5$ ) and observations in WHZ 4 from the non-collared carcass analysis ( $n = 10$ ) because of small sample sizes in these WHZs. We reported the log-odds of the mean and standard deviation of the posterior parameter estimates for each mortality cause category related to the baseline natural mortality category.

For each model, we ran 3 MCMC chains for 10,000 iterations after discarding the first 10,000 iterations as burn-in in program JAGS (JAGS Version 3, [mcmc-jags.sourceforge.net](http://mcmc-jags.sourceforge.net), accessed 6 Sep 2011) through program R (R Version 2.14, [www.r-project.org](http://www.r-project.org), accessed 22 Dec 2011) and R package rjags (rjags Version 3–5, <http://CRAN.R-project.org/package=rjags>, accessed 2 Jan 2012). We assessed convergence by visual inspection of mixing in the chains and using both univariate potential scale reduction factors  $\hat{R}$  (Gelman and Rubin 1992) and the multiple potential scale reduction factor  $\hat{R}^a$ , where  $a$  is the number of parameters (Brooks and Gelman 1998). We judged convergence to be satisfactory when upper 97.5% confidence limits of all  $\hat{R}$ s



**Figure 3.** Boxplots of annual proportion of mortality from 5 causes in collared wolf carcasses and non-collared wolf carcasses in Wisconsin, USA from 2003–2012 (Unk. = unknown mortality sources).

and  $\hat{R}^a$  were  $<1.1$  (Gelman et al. 2003). We assessed model fit with visual and statistical posterior predictive checks and we assessed model prediction by checking for correspondence between future data and posterior predictive distributions (see Model Checking S1, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

*Correction between collared and non-collared carcass datasets.*—We included an additional season index,  $j$  where  $j = 1, 2$  for summer and winter seasons, as defined previously, in the latent variables because of the substantial differences in causes of mortality by season. The required data were a multi-year dataset with collared and non-collared carcass data with various causes of mortality, an annual season-specific estimate of the population size, and the annual season-specific number of radio-collared animals in the population. The population and pup estimate numbers were from the WDNR annual wolf monitoring program (Wydeven et al. 2009, MacFarland and Wiedenhoeft 2013). We used all wolves found dead in Wisconsin in the late growth period (Apr 2003–Mar 2012) as our carcass dataset. We calculated the population count in the winter ( $j = 2$ ) of each year  $i$ ,  $N_{obs_{i,2}}$ , as the mean population count in year  $i$  (e.g., winter population count in 2003/2004 = 373–410;  $N_{obs_{1,2}} = 391$ ). We calculated the population count in the summer of each year  $i$ ,  $N_{obs_{i,1}}$ , as the mean of the winter population count in the previous winter plus the mean of the pup count in the following winter (e.g., pup count in 2004/2005 = 118–192;  $N_{obs_{2,1}} = 391 + 155 = 546$ ). The number of pups in the winter was not estimated in 2009–2012. To calculate the observed population size in these last 3 summer seasons, we used the average proportion of pups in the population in the previous summers (0.38) to calculate the mean expected number of pups.

We assigned beta priors to  $d_{jk}$  for  $k=1, 2, 4, 5$ ,  $d_{jk} \sim \text{beta}(1, 1)$ , and we fixed  $d_{j,3} = 1$  under the assumption that we detected all legal kill mortalities. We specified that the initial values for  $d_{ijk}$  and  $m_{ijk}$  were drawn from uniform distributions:  $d_{ijk} \sim \text{uniform}(0.1, 0.9)$ ;  $m_{ijk} \sim \text{uniform}(0.1, 0.5)$ . We performed all analyses in program JAGS through library rjags in program R. We ran 3 MCMC chains for 20,000 iterations after discarding the first 100,000 iterations as burn-in. We assessed the fit and prediction of our fitted model using the same model checking methods described above (see Model Checking S2, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

## RESULTS

### Case Study

*Mortality causes from carcass data.*—Most deaths in the collared carcass dataset were due to illegal killing (33%) and disease (18%), whereas most deaths in the non-collared carcass dataset were due to vehicle strikes (39%), legal kills (30%), and illegal kills (18%; Table 2). The collared carcass dataset had greater proportion of adults (79% vs. 55%) and fewer yearlings (11% vs. 20%) and pups (10% vs. 25%) compared to the non-collared carcass dataset.

Necropsies were performed on 70% of the collared carcasses and 62% of the non-collared carcasses. The proportion of carcasses that were necropsied varied by mortality cause and period. Over 80% of the natural mortalities were necropsied, compared to 51% and 63% of the legal and vehicle mortalities, respectively. Of the carcasses that were illegally killed, 70% of them were necropsied. By period in wolf recovery, 60%, 85%, and 56% of the carcasses were necropsied in the recovery, early growth, and late growth periods, respectively. Of the 443 cases in which field and necropsy mortality cause diagnoses were available, there were 52 cases in which the mortality cause suspected in the field differed from the cause determined at necropsy.

Most carcasses in the collared and non-collared samples were found during the late growth period (77%; Table 2). There was discernible annual variability in the proportion of carcasses with each mortality cause, especially in the collared carcass dataset (Fig. 3). In particular, the proportion of collared carcasses that was illegally killed ranged from 6% to 82% per year (Fig. 3). We suspect that the non-collared carcass dataset was not as variable because we were consistently unable to detect some mortality causes (e.g., natural mortality) without the aid of telemetry to find carcasses in remote locations. The non-collared carcasses had high proportions of mortality causes from legal kills and vehicle strikes, and these causes had the most annual variation in the non-collared carcass dataset (Fig. 3).

*Patterns in mortality causes.*—We obtained satisfactory convergence criteria for both models. All  $\hat{R}$  and  $\hat{R}^a$  values were  $<1.041$ . The results of the model checking demonstrated reasonable predictions from the model and that the model was consistent with the data (see Model Checking S1, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). We focused our interpretation on the results of the collared carcass analysis in early and late growth periods. The

**Table 2.** Mortality cause for collared and non-collared wolf carcasses found in Wisconsin, USA, from 1 October 1979 to 31 March 2012 during 3 periods of wolf recovery (1979–1995: recovery, 1996–2002: early growth, 2003–2012: late growth).

Dataset	Period	Natural	Illegal	Legal	Vehicle	Other	Total
Collared	Recovery	8	8	3	3	7	29
	Early growth	23	13	3	4	6	49
	Late growth	27	48	20	14	21	130
	Total	58	69	26	21	34	208
Non-collared	Recovery	2	10	0	8	3	23
	Early growth	15	20	2	51	13	101
	Late growth	18	93	196	199	38	544
	Total	35	123	198	258	54	668

non-collared carcass analysis demonstrated some different patterns compared to the collared carcass analysis because of the detection probability biases of non-collared carcasses (Fig. 3). The model-fitted values can be used to derive odds ratios for any baseline set of covariates (see Table S1, Table S2, Example S1, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

Collared yearling carcasses had >5 times the odds of an illegal versus natural mortality compared to adults (see Table S1, Example S1, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). The mortality cause probability estimates for yearling carcasses were higher for illegal killing and lower for legal killing compared to the other age and sex classes. Otherwise, the adult male, adult female, and pup patterns in mortality cause were similar (see Table S1, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). In winter compared to summer, collared carcasses were on average 7–28 times more likely to have a natural or illegal mortality cause compared to a vehicle, unknown, or legal mortality cause (Fig. 4). Vehicle and legal mortality causes were more common in summer than in winter (Fig. 4). In the early growth period compared to the late growth period, collared carcasses were >3 times as likely to have a natural mortality cause instead of another cause (see Table S1, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). In the late growth period, carcasses had lower natural mortality and higher illegal killing probabilities compared to the early growth period (Fig. 4).

Collared carcasses in WHZ 2 and 4 were 5 times as likely to have an illegal versus natural mortality cause in the late growth period compared to carcasses in WHZ 1 (Fig. 4). Wolf harvest zones 1 and 3 had similar mortality cause probability estimates for different covariate combinations. Also, WHZs 2, 4, and 5 had similar mortality cause probability estimates with the exception of WHZ 5 having higher predicted probability of natural mortality and lower probability of illegal mortality in the early and late growth periods compared to WHZs 2 and 4 (Fig. 4).

*Correction between collared and non-collared carcass datasets.*—We obtained satisfactory convergence criteria for both models with all  $\hat{R}$  and  $\hat{R}^a$  values <1.031. The results of the model checking demonstrated reasonable predictions from the model and the model was consistent with the data (see Model Checking S2, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

The average annual mortality rate for collared wolves was 0.235 (SD = 0.021) and the average annual rate of illegal mortality was 0.097. On average the mortality rate was 1.9 times higher in winter (mean = 0.154) than summer (mean = 0.018; see Table S3, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). In winter, 83% of collared wolf mortality was due to natural causes or illegal killing with 4 and 9 times higher natural and illegal mortality, respectively, in winter than summer. Legal mortality causes and unknown mortality causes were 6 times and 2 times, respectively, higher in summer than winter (Fig. 5). Legal mortality occurred almost entirely in the summer season, correspond-

ing to targeted lethal control of wolves trapped and euthanized after livestock depredation events.

The median estimated population size was similar to the observed population size, and the 95% credible interval for the estimated population sizes in every season and year overlapped the observed population size (see Table S4, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). Summed across years, the estimated median number of carcasses on the landscape in summer and winter was 1.7 times and 3.3 times, respectively, the number that were observed and this varied by mortality cause (Table 3).

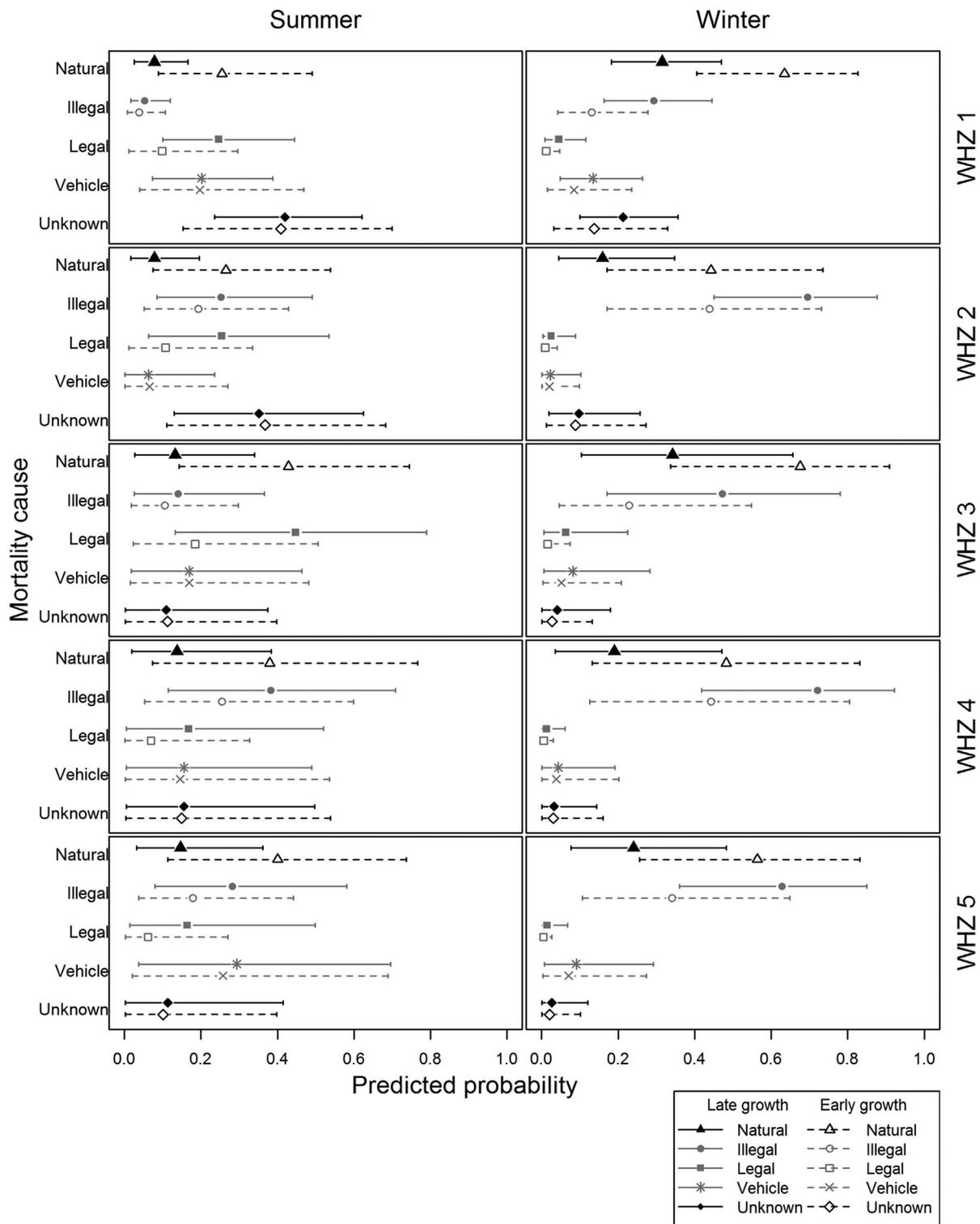
The mean probability of detecting a wolf carcass did not vary by season, except for detection of illegal kill carcasses, which was higher and much more variable in summer than winter (Fig. 6). There were differences in detectability by mortality cause (Fig. 6, see Table S3, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). The highest probability of carcass detection was for legal kills (92%) and vehicle strikes (88%). On average, we detected only 20% of the illegal kill carcasses, 18% of the carcasses with an unknown mortality cause, and 12% of the carcasses with a natural mortality cause (Fig. 6).

## DISCUSSION

We developed methods and provided R code to make long-term records of carcass recoveries more useful to wildlife managers (see R Code S1 and R Code S2, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). We demonstrated how wildlife managers can take a long-term record of carcass data for a wildlife population and understand the spatial, temporal, and demographic patterns in mortality causes. For a sample of radio-collared and non-collared carcass data, managers can calculate the bias in the non-collared carcass dataset compared to the collared carcass dataset to estimate detection probability of carcasses by cause and to estimate the total number of carcasses.

Use of a non-collared sample of carcasses is an appealing way to estimate population parameters because this sample is more convenient, less expensive, and larger compared to collared carcasses. However, non-collared carcasses can be difficult to detect and are subject to biases linked to mortality cause and season (Jennelle et al. 2007). Carcasses with human mortality causes, like vehicle strikes, are often easier to detect than carcasses with natural mortality causes because the former occur in areas more visible to humans. Because of this, a non-collared carcass sample likely is not representative of the causes of mortality in the population. Therefore, the best opportunity to understand the underlying patterns in causes of mortality is by estimating cause-specific detection probabilities for non-collared carcasses that account for these biases. Our manuscript makes this analysis accessible to managers for the first time.

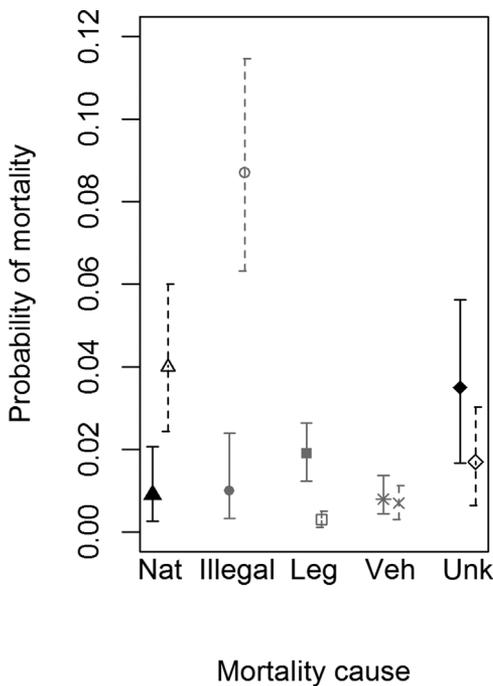
The correction between collared and non-collared carcass datasets may need to be re-examined periodically to accommodate changes to the relationship between these datasets. Using a convenience sample of non-collared carcass recoveries to estimate the number of carcasses on the landscape from previously estimated correction factors is



**Figure 4.** Estimates of mortality cause probabilities for collared adult male wolf carcasses found in 5 wolf harvest zones (WHZs) in Wisconsin, USA in early growth (1996–2002) or late growth (2003–2012) periods during summer (Apr–Sep) or winter (Oct–Mar) from 5 causes of mortality. The gray symbols and bars denote known human-caused mortality sources.

accurate only as long as newly collected recoveries reflect the convenience sample in the previous analysis. A logical time to reassess biases in the non-collared carcass recoveries occurs when there is an additional cause of mortality in the population, like the addition of a harvest season. Re-examination of this relationship requires non-collared carcass

recoveries and radio-collared carcasses collected over the same time period and extent. For the analysis to reflect detection probability of carcasses in the population, the radio-collared animals need to be a representative sample of the population. Analysts often assume that proportional fates of radio-collared animals represent proportional mortality



**Figure 5.** The cause-specific probability of mortality from natural (Nat), illegal, legal (Leg), vehicle (Veh), and unknown (Unk) causes for collared wolves in Wisconsin, USA in summer (solid lines) and winter (dashed lines) from 2003 to 2012. The gray symbols and bars denote known human-caused mortality sources.

causes, but radio-collared recoveries also can be vulnerable to potential biases (Heisey and Fuller 1985, Jacques et al. 2011, Liberg et al. 2012).

Any analysis of carcass recovery data should begin with establishing a standardized procedure and set of definitions that clearly articulates how causes of mortality are assigned to carcasses. Ideally, this process should involve field biologists that assign provisional causes of mortality in the field and pathologists that perform necropsies. Assigning carcasses a single mortality cause simplifies a sometimes-complicated amalgam of health problems identified at necropsy, but it was necessary for the temporal, spatial, and population prediction analyses in this study. Necropsy is invaluable for obtaining accurate mortality causes from carcasses. When there was a discrepancy between a field and necropsy mortality cause assessment in our case study, the necropsy often provided clarity leading to a known mortality cause. As long as a system of rules and definitions is used when making mortality cause assessments, the simplified set of mortality cause categories used for these analyses is appropriate (Heisey and Fuller 1985).

### Case Study

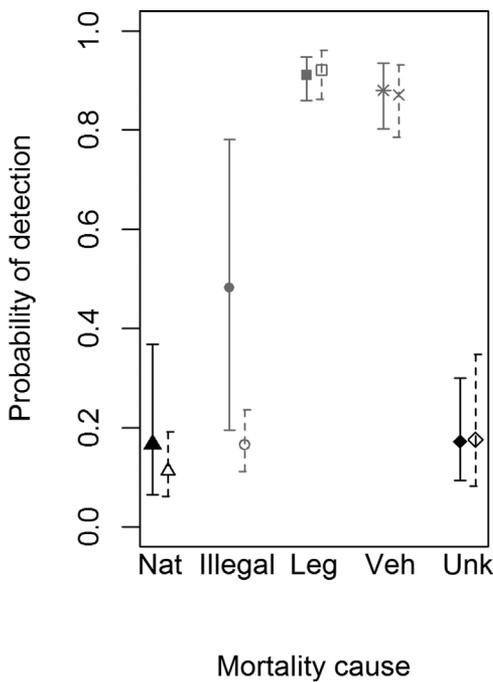
In our case study of 3 decades of carcass recoveries from Wisconsin's wolf population, we detected spatial and temporal patterns that lent insight into population recovery. During 1996–2002, wolves were less likely to have a human-associated mortality cause, perhaps promoting population recovery. During early wolf recovery (Wydeven et al. 1995) and since 2002, wolves were more likely to have an illegal mortality cause, especially in northeastern Wisconsin where there was lower wolf density. Increased illegal mortalities since 2002 could reflect a decline in public support linked to inconsistencies in wolf management resulting from variation in regulatory status of the wolf population under endangered species laws (i.e., federally endangered, federally threatened, removal from endangered species list; Olson et al. 2015). During early wolf recovery, mortality patterns among radio-collared wolves were probably representative, but in recent years (2003–2011) an additional 4% mortality apparently occurred (Stenglein et al. 2015). Some of this additional loss may be illegal killing that is undetected; thus, the proportion of collared carcasses with an illegal mortality cause may be higher than reported (Liberg et al. 2012, Stenglein 2014, Stenglein et al. 2015).

Our analysis is the first to provide direction on which WHZs have the highest rates of human-caused mortality for wolves. Higher proportions of collared wolves had illegal mortality causes in the eastern WHZs (2 and 4) where wolf densities were lower. These areas are preferred wolf habitat (Mladenoff et al. 2009), but the population has increased relatively slowly, suggesting that a higher percentage of illegal killing may have inhibited population growth. To the west, WHZs 1 and 3 had high proportions of natural mortality. Wolves have been established in these WHZs for the longest period and wolf densities are highest, possibly indicating that density-dependent mechanisms may be driving natural mortality. We found WHZs 3, 4, and 5 had the highest proportions of vehicle strikes, presumably because of more agricultural land, more human activity, and higher road density (Stenglein 2014).

Mortality patterns differed by season. Illegal kills and deaths from natural causes (intraspecific strife and disease) were common during winter period (Oct–Mar), which included Wisconsin's fall hunting season for white-tailed deer (*Odocoileus virginianus*) and the time when wolf packs are highly mobile (Mech and Boitani 2003). Of illegal kills of collared wolves, 43% occurred in November; the presence of >600,000 hunters on the landscape during deer gun hunting season in November is clearly a significant factor in the illegal

**Table 3.** The total observed (collared and non-collared) and estimated median number of wolf carcasses (and 95% credible intervals [CI]) recovered during summer and winter 2003–2012 in Wisconsin, USA from 5 mortality causes.

Mortality cause	Summer			Winter		
	Observed	Median	95%CI	Observed	Median	95%CI
Natural	8	48	15–124	33	190	113–292
Illegal	37	63	39–182	102	493	352–667
Legal	186	190	186–202	31	31	30–34
Vehicle	120	125	120–140	91	91	88–102
Unknown	229	229	113–380	91	91	37–174



**Figure 6.** The cause-specific probability of detecting carcasses of wolves that died from natural (Nat), illegal (Illegal), legal (Leg), vehicle (Veh), and unknown (Unk) causes in Wisconsin, USA in summer (solid lines) and winter (dashed lines) from 2003 to 2012. The gray symbols and bars denote known human-caused mortality sources.

killing of wolves. In summer (Apr–Sep), the peak in legal control mortalities corresponds to peak cattle calving season. Cattle are the most common target for livestock depredation by wolves in Wisconsin, and the documented cattle depredations motivate most legal control efforts for wolves (Ruid et al. 2009).

Using the last decade of collared and non-collared wolf carcass data, our correction factor analysis allowed us to quantify the cause-specific bias in the non-collared sample compared to the collared sample, which renders these data more useful. From our case study, we found that vehicle strikes and legal kill mortality causes were the most detectable on the landscape. Estimates of non-collared carcass detections suggest that managers miss more than half of the non-collared carcasses, and our lowest detection was for non-collared carcasses with a natural mortality cause. Our analysis allowed us to estimate that in 2003–2012, more than a third of all carcasses had illegal kill as the mortality cause and more than 400 carcasses with an illegal mortality cause went undetected. Though we expected recovered carcasses with an illegal mortality cause to be low compared to what is on the landscape, an important value of our model is the use of available data to estimate the detection rate and the number of illegally killed wolves that were likely not detected. Our estimate of missing more than 400 illegally killed wolves during 2003–2012 reveals illegally killed wolves as the single largest mortality cause among our mortality cause categories.

The collared carcass sample was most representative of mortality patterns of adult wolves in the heavily forested portions of northern and central Wisconsin where most

wolves were captured and collared (WHZs 1–5). While these areas include most of Wisconsin’s wolf range, those wolves that moved out of these areas into WHZ 6 were probably not represented as well by the collared sample (Mladenoff et al. 2009) and appeared to encounter higher rates of vehicle strikes and illegal kill. Further, the collared carcass recoveries represented only those wolves that were tracked until death. Some collared wolves are lost to follow-up and therefore not included (Stenglein 2014). Our collared sample is unbiased when the loss to follow-up process is independent of the death process (Klein and Moeschberger 2003). However, if some wolves are actually killed and their collars are destroyed when they are lost to follow-up, then we may have bias in our sample. Our collared carcass sample may underestimate the proportion of illegal killing in the population by up to 4% in 2003–2011 (Liberg et al. 2012, Stenglein 2014, Stenglein et al. 2015).

## MANAGEMENT IMPLICATIONS

Managers can make better use of a long-term dataset of carcass recoveries. Better understanding of the number and detection of carcasses by cause can help managers recognize mortality processes in the population and more accurately incorporate mortality into population models that are used for population estimates and harvest management. In our case study of wolves in Wisconsin, the record of radio-collared carcasses confirmed a pattern of proportionally more illegal killing of wolves since 2003 and in the eastern WHZs. Managers could use this information to adjust harvest quotas in areas where wolves are experiencing less illegal killing and, therefore, potentially protecting a segment of the wolf population from high rates of human-caused mortality. Based on the estimated median number of wolf carcasses in 2003–2012, we expect that there were 4 times as many illegally killed wolves than were found and more than a third of all wolves that died were illegally killed. Using available carcass data to estimate the actual number of illegally killed wolves gives us the best information to date on the prevalence of illegal killing in Wisconsin’s wolf population.

## ACKNOWLEDGMENTS

We thank R. Jurewicz, B. Kohn, D. MacFarland, R. Schultz, and D. Thiel for their contributions, and the WDNR pilots who radio-tracked the collared wolves. Thank you to M. Samuel for helpful comments. We thank our sources of funding and support: NSF-IGERT award DGE-1144752: Novel ecosystems, rapid change, and no-analog conditions: the future of biodiversity conservation in human-dominated landscapes, the Wisconsin Department of Natural Resources, the USGS National Wildlife Health Center, U.S. Department of Agriculture, and University of Wisconsin – Madison Department of Forest and Wildlife Ecology. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## LITERATURE CITED

Agresti, A. 2002. *Categorical data analysis*. Wiley-Interscience, New York, New York, USA.

- Agresti, A., and D. B. Hitchcock. 2005. Bayesian inference for categorical data analysis. *Statistical Methods and Applications* 14:297–330.
- Brooks, S., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7:434–455.
- Ciucci, P., G. Chapron, V. Guberti, and L. Boitani. 2007. Estimation of mortality parameters from (biased) samples at death: are we getting the basics right in wildlife field studies? A response to Lovari et al. (2007). *Journal of Zoology* 273:125–127.
- Clark, J. S. 2005. Why environmental scientists are becoming Bayesians. *Ecology Letters* 8:2–14.
- Congdon, P. 2006. Bayesian statistical modelling. John Wiley & Sons, Hoboken, New Jersey, USA.
- Cressie, N., C. A. Calder, J. S. Clark, J. M. V. Hoef, and C. K. Wikle. 2009. Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. *Ecological Applications* 19:553–570.
- Geisser, S. 1984. On prior distributions for binary trials. *American Statistician* 38:244–247.
- Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2003. Bayesian data analysis. CRC press, Boca Raton, Florida, USA.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–472.
- Heisey, D., and T. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *Journal of Wildlife Management* 49:668–674.
- Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management* 70:1544–1555.
- Huso, M. 2011. An estimator of wildlife fatality from observed carcasses. *Environmetrics* 22:318–329.
- Huso, M., and D. Dalthorp. 2014. Accounting for unsearched areas in estimating wind turbine-caused fatality. *Journal of Wildlife Management* 78:347–358.
- Jacques, C., T. Van Deelen, W. Hall, K. Martin, and K. Vercauteren. 2011. Evaluating how hunters see and react to telemetry collars on white-tailed deer. *Journal of Wildlife Management* 75:221–231.
- Jennelle, C., E. Cooch, M. Conroy, and J. Senar. 2007. State-specific detection probabilities and disease prevalence. *Ecological Applications* 17:154–167.
- Joly, D., D. Heisey, M. Samuel, C. Ribic, N. Thomas, S. Wright, and I. Wright. 2009. Estimating cause-specific mortality rates using recovered carcasses. *Journal of Wildlife Diseases* 45:122–127.
- Klein, J. P., and M. L. Moeschberger. 2003. Survival analysis: statistical methods for censored and truncated data. Springer-Verlag, New York, New York, USA.
- Korner-Nievergelt, F., O. Behr, R. Brinkmann, M. A. Etterson, M. M. P. Huso, D. Dalthorp, P. Korner-Nievergelt, T. Roth, and I. Niermann. 2015. Mortality estimation from carcass searches using the R-package carcass—a tutorial. *Wildlife Biology* 21:30–43.
- Liberg, O., G. Chapron, P. Wabakken, H. C. Pedersen, N. T. Hobbs, and H. Sand. 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B: Biological Sciences* 279:910–915.
- MacFarland, D., and J. E. Wiedenhoef. 2013. Wisconsin gray wolf post-delisting monitoring: 27 January 2012 through 14 April 2013. Bureau of Wildlife Management, Wisconsin Department of Natural Resources, Madison, USA.
- Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1–34 in L. D. Mech, and L. Boitani, editors. *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, Illinois, USA.
- Mladenoff, D. J., M. K. Clayton, S. D. Pratt, T. A. Sickley, and A. P. Wydeven. 2009. Change in occupied wolf habitat in the northern Great Lakes region. Pages 119–138 in A. P. Wydeven, T. R. Van Deelen, and E. J. Heske, editors. *Recovery of gray wolves in the Great Lakes region of the United States: an endangered species success story*. Springer, New York, New York, USA.
- Ntzoufras, I. 2009. Bayesian modeling using WinBUGS. John Wiley & Sons, Hoboken, New Jersey, USA.
- Olson, E. R., J. L. Stenglein, V. Shelley, A. R. Rissman, C. Browne-Núñez, Z. Voyles, A. P. Wydeven, and T. Deelen. 2015. Pendulum swings in wolf management led to conflict, illegal kills, and a legislated wolf hunt. *Conservation Letters* 8: in press.
- Paap, R. 2002. What are the advantages of MCMC based inference in latent variable models? *Statistica Neerlandica* 56:2–22.
- Peron, G., J. Hines, J. Nichols, W. Kendall, K. Peters, and D. Mizrahi. 2013. Estimation of bird and bat mortality at wind-power farms with superpopulation models. *Journal of Applied Ecology* 50:902–911.
- Pollock, K., S. Winterstein, C. Bunck, and P. Curtis. 1989. Survival analysis in telemetry studies - the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- Roffe, T. J., and T. M. Work. 2005. Wildlife health and disease investigations. Pages 616–631 in C. E. Braun, editor. *Techniques for wildlife investigations and management*. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.
- Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press, Burlington, Maryland, USA.
- Ruid, D. B., W. J. Paul, B. J. Roell, A. P. Wydeven, R. C. Willging, R. L. Jurewicz, and D. H. Lonsway. 2009. Wolf-human conflicts and management in Minnesota, Wisconsin, and Michigan. Pages 279–295 in A. P. Wydeven, T. R. Van Deelen, and E. J. Heske, editors. *Recovery of gray wolves in the Great Lakes Region of the United States: an endangered species success story*. Springer, New York, New York, USA.
- Schaub, M., and R. Pradel. 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. *Ecology* 85:930–938.
- Stenglein, J. L. 2014. Survival of Wisconsin's gray wolves from endangered to harvested, 1980–2013. Dissertation, University of Wisconsin - Madison, Madison, USA.
- Stenglein, J. L., J. Zhu, M. K. Clayton, and T. R. Van Deelen. 2015. Are the numbers adding up? Exploiting discrepancies among complementary population models. *Ecology and Evolution* 5:368–376.
- Stevens, B. S., and B. Dennis. 2013. Wildlife mortality from infrastructure collisions: statistical modeling of count data from carcass surveys. *Ecology* 94:2087–2096.
- Thiel, R. P., W. Hall Jr, E. Heillhecker, and A. P. Wydeven. 2009. A disjunct gray wolf population in Central Wisconsin. Pages 107–117 in A. P. Wydeven, T. R. Van Deelen, and E. J. Heske, editors. *Recovery of Gray wolves in the Great Lakes Region of the United States: an endangered species success story*. Springer, New York, New York, USA.
- Tsai, K., K. Pollock, and C. Brownie. 1999. Effects of violation of assumptions for survival analysis methods in radiotelemetry studies. *Journal of Wildlife Management* 63:1369–1375.
- U.S. Geological Survey, and Upper Midwest Environmental Sciences Center. 2005. USGS Gap Analysis Program - Wisconsin Stewardship Data. U.S. Geological Survey, La Crosse, Wisconsin, USA.
- U.S. Department of Commerce. 2010. TIGER/Line Files. U.S. Department of Commerce U.S. Census Bureau Geography Division, Washington, D.C., USA.
- Van Deelen, T. R. 2009. Growth characteristics of a recovering wolf population in the Great Lakes region Pages 139–153 in A. P. Wydeven, T. R. Van Deelen, and E. J. Heske, editors. *Recovery of gray wolves in the Great Lakes Region of the United States: an endangered species success story*. Springer, New York, New York, USA.
- Wisconsin Department of Natural Resources. 1998. Wisconsin Initiative for Statewide Cooperation on Landscape Analysis and Data (WISCLAND) land cover. Wisconsin Department of Natural Resources, Madison, USA.
- Wydeven, A. P., R. N. Shultz, and R. P. Thiel. 1995. Monitoring of a recovering gray wolf population in Wisconsin, 1979–1991. Pages 147–156 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Edmonton, Alberta, Canada.
- Wydeven, A. P., J. E. Wiedenhoef, R. N. Schultz, R. P. Thiel, R. L. Jurewicz, B. E. Kohn, and T. R. Van Deelen. 2009. History, population growth, and management of wolves in Wisconsin. Pages 87–105 in A. P. Wydeven, T. R. Van Deelen, and E. J. Heske, editors. *Recovery of gray wolves in the Great Lakes Region of the United States: an endangered species success story*. Springer, New York, New York, USA.

Associate Editor: John Squires.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.